Contents lists available at ScienceDirect

Trees, Forests and People

journal homepage: www.sciencedirect.com/journal/trees-forests-and-people

Seeing yew for the forest: a call to action for improving conservation and restoration of the European yew (*Taxus baccata* L.)

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https://doi.org/10.1016/j.tfp.2025.101093

ARTICLE INFO

Keywords:
Taxus baccata L.
Conservation
Long-term history
Current dynamics
Ecological resilience
Restoration ecology
Priority research questions

ABSTRACT

The European yew (*Taxus baccata* L.) is a long-lived conifer of ecological, cultural, and historical importance across Eurasia. Despite its remarkable resilience, wide distribution, and symbolic importance, the species has experienced a long-term decline due to a complex interplay of climatic fluctuations, megafaunal extinctions, human exploitation, and insufficient regeneration. Recent studies in palaeoecology, archaeology, dendroecology, and conservation have revealed a species with greater ecological plasticity and a broader historical distribution than previously assumed. However, many fundamental questions remain unresolved, particularly regarding its biogeographical history, population dynamics, recruitment processes, and the drivers of its decline.

This review stems from prior investigations of yew in the French Pyrenees and, more broadly, across Europe. These efforts led to a transdisciplinary seminar and opened a collaboration uniting >30 researchers across Eurasia. By synthesizing a wide array of data and perspectives, the article highlights key knowledge gaps and outlines emerging research priorities. These are organized thematically—past, present, and future—and include 25 questions on the species' ecological niche, life-history strategies, human interactions, genetic resilience, and conservation under global change. The article advocates for a shift towards integrative and long-term conservation strategies that embrace the historical legacies of yew populations, the general ecology of the species along with local ecological context dependence, and the urgency of future threats. By identifying pressing research needs, this review seeks to lay the foundation for new collaborative initiatives and to support evidence-based conservation of this emblematic yet understudied species.

1. Introduction

The European yew (*Taxus baccata* L.), also known as common yew, is a long-lived, slow-growing conifer native to temperate and Mediterranean Eurasia, spanning from the Atlantic fringe to the Caucasus and northern Iran (Calvia et al., 2024; Esmailzadeh and Hosseini, 2007; Gholizadeh et al., 2020; Kalantari et al., 2022; Karami-Kordalivand et al., 2021; Laliga and Martí, 2012; Romo et al., 2017; Schirone et al., 2010; Thomas and Polwart, 2003). The preferential niche of yew seems to correspond to a mild oceanic climate characterized by relatively mild winters, abundant rainfall and high humidity (Thomas and Polwart, 2003). However, yew can also thrive under more continental, Mediterranean, or montane conditions. A growing body of palaeoecological, ecological, archaeological, and genetic studies has revealed a species more ecologically versatile and historically widespread than previously assumed (Kvaratskhelia and Gavashelishvili, 2025; Mayol et al., 2015; Thomas and Polwart, 2003; Uzquiano et al., 2014). However, significant gaps persist in our understanding of the interactions between yew and past climates, megafauna, forest dynamics, and humans. Likewise, current conservation strategies often lack integration of long-term ecological knowledge, genetic diversity assessments, and landscape-scale management approaches.

Moreover, despite its ecological singularity (Mayol et al., 2015), wide biogeographic range (Thomas and Polwart, 2003), and deep-rooted cultural importance (Delahunty, 2007), this species has experienced a long-term decline, the causes of which remain poorly documented and under-studied. While yew exhibits remarkable adaptability and physiological tolerance to shade and drought, it suffers from poor regeneration and high sensitivity to environmental changes, herbivory, and competition (Hageneder, 2007; Niinemets and Valladares, 2006; Svenning, 2003). The species' decline is compounded by anthropogenic pressure, including historical overexploitation for its wood, shifts in forest management, eradication linked to its toxicity for livestock, and recent climate change which have resulted in habitat loss and fragmentation (Piovesan et al., 2009; Rudow, 2001; Svenning and Magård, 1999). Yet, paradoxically, yew is not systematically protected across its native range, even though it is included in threatened species lists and in the European Habitats Directive (92/43/EEC) (EEC 22/07/1992) under three habitat types, two of which of priority importance: "Mediterranean *Taxus baccata* woods 9580*", "Apennine beech forest with *Taxus* and *Ilex* 9210*" and "Atlantic acidophilous beech forests with *Ilex* and sometimes also *Taxus* in the shrub layer 9120" (Katsavou and Ganatsas, 2012). As stated by Hageneder (2007), how can a tree species that is included in the lists of threatened species in many countries, yet, at the same time, not be protected in these same regions?

In recent decades, yew has therefore attracted renewed scientific interest, as key questions regarding its historical biogeography, population dynamics, ecological role within forest socio-ecosystems, patterns of decline, the drivers behind its reduced potential distribution, and the development of effective conservation strategies remain unresolved (Hageneder, 2007; Schirone et al., 2010). The exceptional adaptability of yew may explain why it is the oldest tree species in Europe (Hageneder, 2007), but it also raises many questions about its decline over several thousand years.

A plethora of research projects are being conducted, to fill the gaps of knowledge about this species. The several publications in the form of bibliographic summaries and/or new treatments of existing data, which, while essential for assessing the state of knowledge, highlight the gaps that require further research (Balaguer-Romano et al., 2022; Benham et al., 2016; Casals et al., 2015; Ghanbari et al., 2019; Hao et al., 2008; Linares, 2013; Mayol et al., 2015; Pérez-Díaz et al., 2013; Sanchez-Martinez et al., 2021; Schnitzler et al., 2023; Thomas and Polwart, 2003; Uzquiano et al., 2014). Moreover, over the past two decades, several yew dedicated symposia have been organized to address some research areas: biogeography, conservation genetics, paleoecology, and species restoration. For example, the 1st to 4th International Conferences on Yew were held in Alcoi (2006), Olot (2008), Ponferrada (2010), and Poblet (2014), respectively. Additionally, the 1st International Conference on Yew of Turkey was held in Düzce in 2015.

In November 2023, the GEODE laboratory organized its first seminar on "Science and territory: past and future landscapes", focusing on yew trees. The seminar brought together researchers and local stakeholders with a passion for this species. Various presentations highlighted gaps in our knowledge, while the round table discussion underscored the need for answers to effectively plan future management and conservation strategies for this species. All presentations and discussions drew on ongoing research, observations and in-depth literature reviews related to participants' research interests. By synthesizing disparate areas of knowledge and expertise, we have established a consortium of researchers studying this taxon across Eurasia. This consortium of experts presents this opinion paper with the aim of reviewing the current state of knowledge on the history, ecology and role of yew in the ecosystem, its use by societies, a forward-looking section and, finally, the management and conservation actions implemented. The priority research issues that should, in this author's opinion, be studied in greater depth to improve our knowledge and support more effective conservation of the species are identified and presented in the form of questions at the beginning of each section. Beyond synthesizing current knowledge, the present article aims to serve as a scientific foundation for future collaborative

projects and funding applications at national, and international levels for advancing our understanding and conservation of this emblematic species.

2. Methodology

In the Pyrenees, the discovery of numerous yew macroremains prompted the GEODE laboratory to conduct sustained research over the past decade to better characterize the history, niche evolution, and current distribution of the species in this mountain range, where yew is now rare and largely confined to rocky cliffs. Building upon these initiatives, GEODE organized a seminar on October 30–31, 2023, in Toulouse. This seminar brought together researchers and forest managers to exchange knowledge and develop strategies for advancing yew research and restoration in mountain ecosystems. The event convened four leading experts on yew from complementary disciplines: palaeoecology (Jacques-Louis de Beaulieu), archaeobotany (Koen Deforce), plant architecture (Yves Caraglio), and forest ecology (Annick Schnitzler). Their presentations, along with a synthesis of ongoing work by the lead author, were followed by a roundtable discussion involving scientists, stakeholders, and forest managers. This preliminary exchange highlighted the significant lack of integrated knowledge regarding the species' long-term history, current ecology, dynamics, and conservation, and served as the starting point for this collective effort.

In the aftermath of the seminar, a broader scientific consortium gradually coalesced, drawing upon the professional networks of the invited experts. The group expanded to include 30 researchers from various geographical regions across Eurasia, representing a wide range of academic disciplines, including dendroecology, historical ecology, conservation biology, and genetics. Regular online meetings were held to foster exchange and collaboration. The initial two meetings centered on the introduction of the consortium and the identification of overarching objectives for advancing new research. After careful consideration, it was decided that a synthesis paper would be prepared to identify significant knowledge gaps. This paper will serve as a foundation for future collaborative projects.

Three subsequent meetings were dedicated to defining the structure, scope, and framework of the paper, as well as refining the research questions considered most critical. These collaborative discussions, informed by participants' expertise and an extensive literature review conducted by the lead author, led to the identification of key research priorities concerning yew. The integrative literature review is based on a comprehensive screening of peer-reviewed articles, gray literature, and historical sources, undertaken between 2023 and 2025, to synthesize the current state of knowledge on yew. More than 1500 documents were identified across major academic databases using the terms "Taxaceae", "Taxus", "Taxus baccata", or "yew" combined with thematic keywords corresponding to identified research gaps (e.g., "interglacial decline drivers," "sexual dimorphism," "endangered," "threats," etc.). Each proposed question was discussed collectively during the organized meeting and evaluated according to its scientific relevance, feasibility, and potential contribution to conservation or management practices. The prioritization process relied on open discussion and consensus-building rather than formal voting, and the final list of 25 questions was established through unanimous agreement among all participants, ensuring balanced representation across disciplinary perspectives. Over 600 documents were retained and analyzed, of which 132 are cited in the final text. Although the initial outline was drafted by the lead author, the entire consortium contributed to its refinement through iterative feedback and collective expertise.

3. Identified knowledge gaps and emerging research questions (Table 1)

3.1. Past

3.1.1. Long-term history

The evolutionary and biogeographic history of yew during the Pleistocene provides important insights into its resilience, but this history remains only partially documented. While genetic evidence indicates that the yew persisted in multiple western Eurasian refugia, their precise location, extent, and connectivity are still debated (Möller et al., 2020; Spjut, 2007a). Palaeoecological data indicate recurrent expansions of the yew distribution during interglacial periods while some contractions into refugia during glaciations (Avcı, 2014; De Beaulieu et al., 2001; Gholizadeh et al., 2020; Koç et al., 2018; Svenning et al., 2008). During certain interglacial periods, yew occupied a wider geographic distribution, being more abundant and expanding its geographic range much further, such as during the Eemian (De Beaulieu et al., 2001; Deforce and Bastiaens, 2007; Mayol et al., 2015; Müller et al., 2003; Pearce et al., 2024; Turner, 2000)(De Beaulieu et al., 2001; Deforce and Bastiaens, 2007; Mayol et al., 2015; Müller et al., 2003; Pearce et al., 2024; Turner, 2000). However, during some other interglacials, yew appears to be as discrete as during the Holocene (Deforce and Bastiaens, 2007). The interpretation of these divergent dynamics is still complicated due to the limited and patchy distribution of reliable records (Table 1 – Q1).

Pollen is the primary source of evidence, but *Taxus* pollen has limited dispersion capacities, and is often poorly preserved. Consequently, yew is frequently underrepresented in pollen diagrams resulting in an underestimation of its historical abundance and distribution (Noryskiewicz, 2003; Thomas and Polwart, 2003). This is demonstrated by finds of macrofossils, archaeological artefacts and other proxies revealing its presence at several sites where palynological data do not reflect it (Bal et al., 2023; Milks, 2020; Oakley et al., 1977; Saulnier et al., 2020; Thieme and Veil, 1985). This discrepancy indicates that the apparent marginality of yew in some reconstructions may be as much due to methodological limitations as to its actual rarity (Table 1 – Q2).

The distribution of yew across interglacial periods is still challenging to interpret (see Table 1 – Q1). During the Eemian, when yew appears to have reached its greatest extent, favorable climatic conditions are often cited as a major driver of its expansion. However, climate alone cannot fully account for this pattern, as similarly mild and humid conditions would also have benefited competing tree species, potentially limiting yew's dominance in closed-forest settings. Therefore, alternative explanations point to biotic interactions, particularly the potential role of large herbivores in maintaining semi-open forest structures through browsing and disturbance (Pearce et al., 2024). Such processes may have created regeneration niches and enhanced local dispersal of yew, although this remains largely speculative and lacks empirical testing at broader spatial scales (Table 1 – Q3).

During the Pleistocene-Holocene transition, megafauna populations experienced a significant decline due to a combination of climatic and anthropogenic pressures, leading to the extinction of many species. During the Holocene, in many parts of Eurasia, the maximum detection of yew occurs during the Atlantic period and Subboreal periods, when climatic conditions were warm and humid (Wengler and Vernet, 1992). This period also coincides with the maximum forest cover, the development of forest fauna, the transition of hunter-gatherer groups to sedentary lifestyles, the introduction of agriculture and livestock farming, and a more intensive exploitation of environmental resources. This Holocene yew optimum revealed by pollen sequences appears considerably lower than during some of the preceding interglacial periods (Pearce et al., 2024). In France, while palynological studies have rarely identified yew in sedimentary archives from the southern Alps, Provence and the central Pyrenees, archaeological and pedoanthracological remains show that the species has been present in these regions

Table 1
Overview of the main research questions identified in this review. These questions highlight the principal knowledge gaps concerning the ecology, biogeography, and management of Taxus baccata and outline promising directions for future research and conservation efforts across Eurasia.

Section	Question number	Priority research questions
Past	**Q1**	How did climatic conditions, competition, and disturbance dynamics (or other driving forces) shape the expansion patterns of Taxus baccata during successive interglacial periods?
	Q2	Would it be possible to refine our knowledge of the extent of yew distribution in the past using other than palynological data (seed, charcoal, leaves, etc.) or archive types?
	Q3	Would it be possible to ascertain the hypothesis that megafauna and large herbivores played a significant role in the distribution of yew trees?
	Q4	To what extent has anthropogenic pressure contributed to the historical decline of yew across Eurasia, and have these pressures been spatially consistent?
	Q5	What is the (co-evolutionary) relationship between yew and humans since the onset of a regionally strong human impact since the mid-Holocene?
	Q6	Could the loss of this species lead to the disappearance of knowledge about its potential uses in medicine?
Present	**Q7**	How factors that have historically influenced the contraction of yew's distribution can be disentangled to reconstruct the potential niche of yew?
	Q8	How can yew's sensitivity to climatic variables be leveraged for climate reconstruction and forecasting its future distribution?
	Q9	To what extent do climatic and edaphic conditions constrain the ecological niche of yew across different biogeographic regions?
	Q10	How do interactions with co-occurring tree species influence the realized niche, resilience, and regeneration potential of yew across different forest communities?
	Q11	How do environmental heterogeneity and resource availability influence sex ratios and sexual dimorphism across habitats?
	Q12	What are the evolutionary and ecological consequences of vegetative propagation methods, and how do they interact with sexual dimorphism, herbivory, and vegetative reproduction to shape genetic diversity and population dynamics?"
	Q13	To what extent are suppressed yew recruits able to respond to canopy openings and successfully reach the overstory, and under which ecological or disturbance conditions can this process lead to the development of dominant or even monospecific yew stands?
	Q14	What combinations of abiotic, biotic, and anthropogenic factors enable yew to form monospecific stands, and what implications does this have for the ecological and genetic resilience of these populations
	Q15	How would deer exclusion affect yew regeneration dynamics and competitive interactions with other tree species?
	Q16	Can we improve our knowledge of the ecosystem services (biodiversity, regulation, etc.) provided by yew trees, either as companion or dominant species?
Future	**Q17**	How does climate change influence the current and future distribution of yew?
	Q18	To what extent might anthropogenic climate warming create ecological conditions analogous to past interglacial optima, and could such conditions favor the expansion of yew populations in northern Europe and at higher elevations?
	Q19	What are the current levels and spatial patterns of genetic diversity in yew populations across their range, and how can conservation and restoration strategies be designed to maintain or enhance this diversity?
	Q20	To what extent could the exclusion of deer fundamentally change long-term forest dynamics, and what implications might this have for the regeneration and persistence of yew populations?
	Q21	Could the restoration of functional faunas (megafaunas and large carnivores) counteract the negative effect of deer and improve the natural regeneration of yew by creating heterogeneous semi-open vegetation structures?
	Q22	Which management or no management practices or are most effective in promoting yew regeneration in different ecological contexts?
	Q23	what role should genetic origin and adaptive diversity play in guiding the future restoration and conservation of yew across Europe's fragmented landscapes?
	Q24	How can yew be integrated into (trophic) rewilding efforts?
	Q25	Might the unexpected proliferation of sub-spontaneous yews in urban and peri-urban contexts herald a new phase in the species' European distribution, thereby challenging conventional distinctions between relict populations of natural origin and novel, human-mediated occurrences?

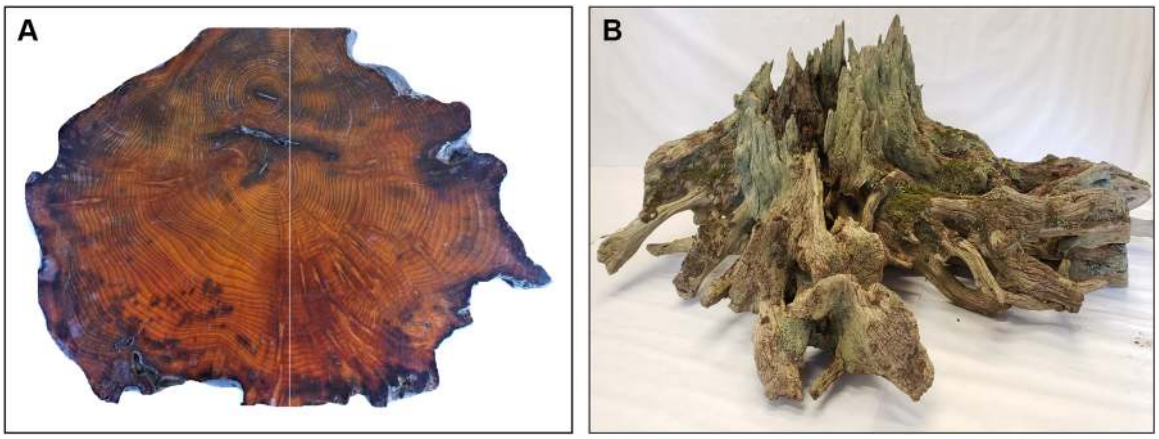


Fig. 1. Examples of the prehistoric and historical record of yew extracted from geoarchives in north-eastern Germany. (A) Stem cross section of yew (20 cm diameter) extracted 1979/1980 from the Hütelmoor peatland in the Rostocker Heide forest directly on the Baltic Sea coast (photograph: Franz Kokesch). It dates according to a radiocarbon age to approx. 4000 years cal BP. (B) Yew stump with root plate (110 cm diameter) in the Darss Museum at Prerow (photograph: Annett Geldschläger). The historical stump was found and excavated in the forest soil on the Darss peninsula, Baltic Sea coast, in the 1950s.

since the Atlantic period (Bal et al., 2023; Robin et al., 2021; Saulnier et al., 2020). This discrepancy in the data underscores the necessity to investigate the role of alternative proxies in reconstructing the historical niche of yew trees (Table 1 – Q2).

The Atlantic to Subboreal optimum of yew was followed by a gradual decline of the species over the subsequent millennia. In England, the recent work from Bebchuk et al. (2023) suggest that the still debated 4.2 ka event, leading to sea level rise and marine inundation of coastal lowlands, may have strongly contributed to the yew decline as already observed for oak and pine. But it is highly likely that also certain non-climatic factors have played a significant role as a direct or indirect catalyst in the decline of the yew since the middle of the Holocene, such as the development (and settlement) of human societies (Bebchuk et al., 2023; Hageneder, 2007; Kaiser et al., 2024; Saulnier et al., 2020; Thomas and Polwart, 2003). The Neolithic transition, marked by the shift toward sedentary lifestyles, led to extensive forest openings, particularly in mountainous regions, often through the recurrent use of fire. Because of its thin bark, yew is especially sensitive to fire damage (Pearce et al., 2024). In addition, yew was intensively exploited by early societies, both for its high-quality wood and for the medicinal or toxic properties of its foliage. Although yew remains are systematically found—albeit with variable frequencies—in archaeological and palaeobotanical assemblages, its abundance appears to have reached a minimum from Antiquity onward (Martin and Thiébault, 2010; Saulnier et al., 2020). The role of human societies in the dynamics and distribution of yew trees remains a little-explored and difficult-to-grasp subject (Martin and Thiébault, 2010) (Table 1 – Q4).

3.1.2. Human societies-yew interactions

The discovery of numerous archaeological artifacts made from yew illustrates the significant value placed on this wood resource for a multitude of uses (Fig 1A, B) (Bjurhager et al., 2013; Edinborough, 2005). Some of the earliest known wooden artifacts are spears made of *Taxus*, including one unearthed in Clapton, England, estimated to be 400 000 years old (Oakley et al., 1977), and at Lehringen in Lower Saxony in Germany, to Eemian 5e, i.e. approx. 124,000–119,000 years ago (Hageneder, 2007; Milks, 2020; Thieme and Veil, 1985). Yew was employed not only in the fabrication of spears, but also in the production of bows, due to the flexibility of yew wood (Bjurhager et al., 2013; Clark, 1963; Edinborough, 2005; Haneca et al., 2022). The high demand from the English army in the Middle Ages for long yew bows is advanced to have been the primary cause of the species' decline in Great Britain, and maybe in parts of Western and Central Europe. Indeed, whether in England or Bosnia-Herzegovina, there is abundant textual evidence indicating that thousands of yew trees were felled, primarily for the purpose of manufacturing weapons. The necessity for this wood even resulted in the establishment of an untenable trade between English kingdom and private trading companies from other European countries, pushing the species towards extinction in Europe (Hageneder, 2007; Hartzell, 2021). Prussia and Bavaria attempted to impose restrictions on the yew trade, but these measures were not successful in achieving lasting results. But the precise geographical limits of this trade in yew wood to England remain uncertain (Table 1 – Q4).

However, the yew tree's remarkable capacity for resprouting from the stump continuously may have enabled the sustainable harvesting of wood for weaponry without the need for systematic cutting of the trees. While numerous recent studies have also revealed that societies since the Metal Age implemented early forms of "forest management" to ensure the sustainability of wood resources, it is essential to study in greater depth the real impact of this high demand on the distribution of the species. It is also crucial to investigate whether archives could indicate the existence of systematic management of this resource during historical periods. Archaeological evidence also shows that yew wood was used for a wide range of other purposes. These include the manufacture of wooden tools such as axe handles, bows, and pointed sticks (Haneca and Deforce, 2020; Uzquiano et al., 2014), as well as more occasional uses like charcoal production in the Romanian Carpathians and the Pyrenees (Fouédjeu et al., 2021; Py-Saragaglia et al., 2025, 2017), the crafting of containers for dairy products (Cherel, 2022), and even tar extraction (Cywa, 2018; Haneca et al., 2022). This long-term interaction between human societies has been documented only locally, while evidence of the versatile use of yew trees dates to the Pleistocene and increased during the Neolithic period. A more profound understanding of the co-evolution between yew trees and past societies could serve as a catalyst for their future management (Table 1 – Q5).

The high toxicity of certain metabolites probably contributed to the deliberate eradication of certain populations (Thomas and Polwart, 2003). While the plant's leaves, twigs or bark are consumed by deer (to a lesser extent by deer roe, Mysterud and Østbye, 2004), there has been recorded cases of cattle and horses suffering from the plant's toxicity, leading to death (Wilson and Hooser, 2018). However, archaeological evidence from various parts of Europe indicates that yew branches and twigs were deliberately used as litter in sheepfolds and cattle shelters for two primary reasons: first, due to their insecticidal and antimicrobial properties, and second, potentially as a method to gradually immunize livestock against yew toxicity from an early age and supplement their diet (Delhon et al., 2008; Martin and Thiébault, 2010; Thomas and Polwart, 2003). Although ancient and medieval scholars were already

aware of its toxicity (Cywa, 2018), yew has simultaneously been regarded across many countries as a symbol of longevity and cultural heritage. This dual perception is rooted in its strong symbolic significance, which spans both early European pagan traditions and Christian iconography (Casier et al., 2024; Hageneder, 2007; Szczepanik, 2020). Within Bosnia and Herzegovina, the yew has been employed in numerous ritualistic practices, including its incorporation in house construction with the intention of promoting longevity, the use of amulets for clothing and working animals, and other similar applications (Ballian and Kraigher, 2021). Since antiquity, medicinal properties of the yew have been widely acknowledged (Hageneder, 2007). Indeed, some chemical constituents present in the form of alkaloids, flavonoids, and essential oil in some parts of the tree exhibit a range of properties, some of which are beneficial for medicinal purposes: antispasmodic, cardiotonic, diaphoretic, emmenagogue, expectorant, narcotic and purgative (Sharma et al., 2021). The paclitaxel (Taxol), a specific medical constituent present in yew shoots, has been developed into cancer treatments, due to its ability to inhibit cell proliferation (Hageneder, 2007; Malik et al., 2011). The full medicinal potential of yew trees, especially their various chemical compounds and how they might be used in modern pharmacology, is still an area of active research (Sharma et al., 2021) (Table 1 – Q6).

3.2. *Present*

3.2.1. *Ecological niche*

The current distribution range of the yew tree is undoubtedly a remnant of its former range (Cedro, 2023; Cedro and Iszkuło, 2011; Thomas and Polwart, 2003). Today, it extends from the shores of the Caspian Sea to Norway, and from plains to high altitudes encompassing a large variety of forest associations and abiotic contexts (Ballian and Kraigher, 2021). Yew is also well-established on Mediterranean islands such as Sardinia and Corsica, as well as oceanic islands such as Azores, Britain and Ireland. In Bosnia and Herzegovina, yew populations occur across a marked climatic gradient, from sub-Mediterranean areas with a Mediterranean climate to Pannonian regions under continental (Ballian and Kraigher, 2021). Such environmental heterogeneity is reflected in pronounced phenotypic diversity, even over short distances (Ballian and Kraigher, 2021; Spjut, 2007b). For instance, studies in the north-western Balkans report significant variation among populations in needle morphology—such as needle area and the position of maximal width—and highlighted distinct clusters corresponding to separate genetic lineages (Dinaric vs. continental) (Tumpa et al., 2022). Despite this diversity, it remains unclear which factors—climatic constraints, historical land use, biotic interactions, or dispersal barriers—have most strongly shaped the

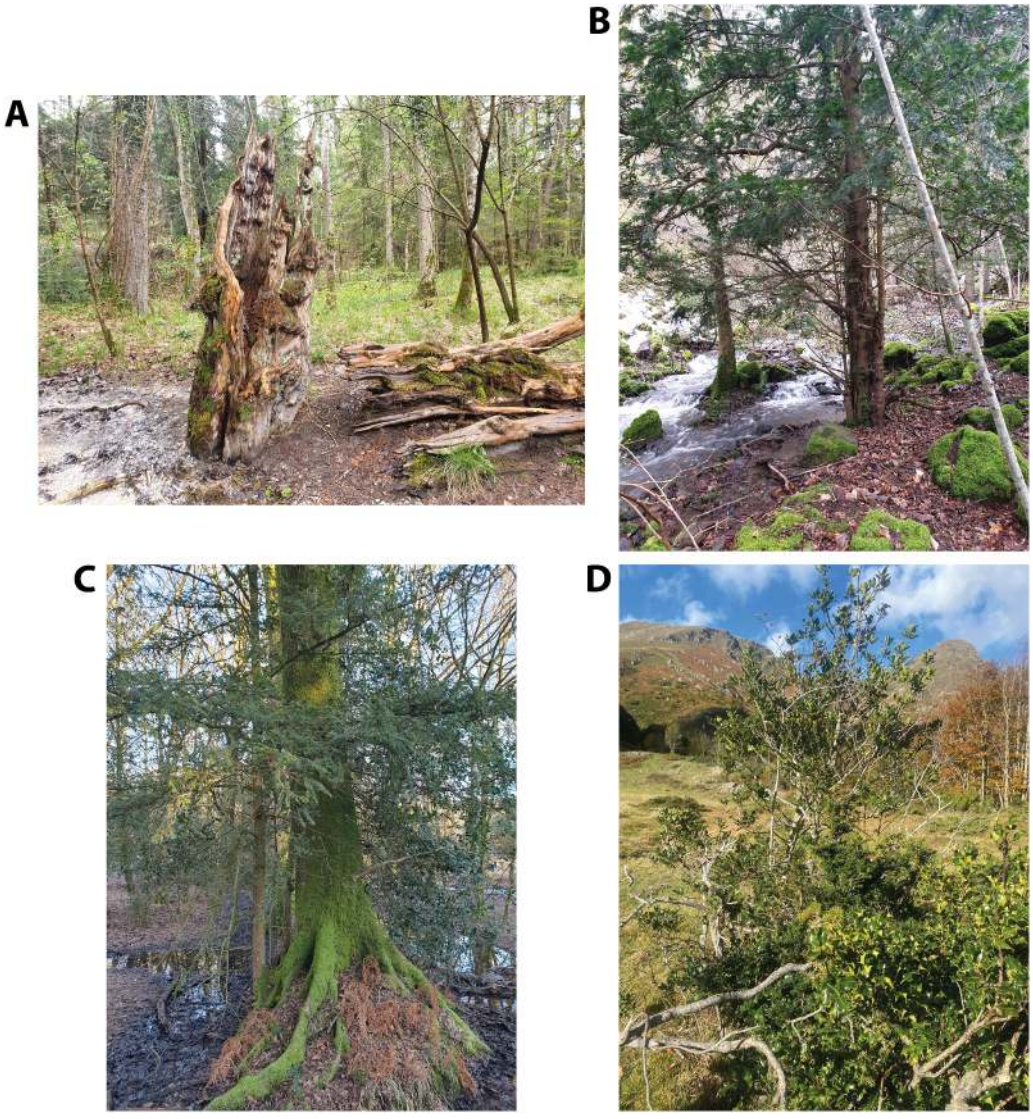


Fig. 2. Photographs of yews thriving or having thrived on moist soils:(A) in Germany (© Schnitzler A.), (B) in Vosges mountains (© Schnitzler A.), (C) in Brittany (© Schnitzler A.), (D) in the central Pyrenees in the Bernadouze peatbog (© Saulnier M.).

contraction of yew's range. Disentangling their relative influence is essential to reconstruct the species' potential niche and to evaluate its capacity to respond to future environmental change (Table 1 – Q7).

The primary climatic factors that influence the species are adequate humidity and moderate annual temperatures, particularly during the winter months (Ahmadi et al., 2020). This high sensitivity to climate makes yew an excellent candidate for reconstructing climate from its growth rings (Galvin et al., 2014; Kvaratskhelia and Gavashelishvili, 2025; Seyfullayev et al., 2021). Yew's growth rings have shown responsiveness to climatic factors, particularly precipitation and temperature. In southern England, yew tree-ring widths correlate strongly with precipitation totals and drought indices, indicating their potential as proxies for hydroclimate reconstructions (Bebchuk et al., 2023). Further research could enhance our understanding of past and future climate dynamics through yew dendrochronology (Table 1 – Q8)

Substrate characteristics do not appear to be a significant factor in the successful establishment of the yew, as it can thrive in a variety of soil types (Ballian and Kraigher, 2021; Calvia et al., 2024; Karami-Kordalivand et al., 2021; Thomas and Polwart, 2003). Furthermore, both relict occurrences and palaeoecological records in North-East Germany indicate that all occurring substrates were colonized by yew ranging from carbonate sedimentary rock (chalk), glacial till, acidic dune and fluvial sands to peat (Kaiser et al., 2024). Yew was probably once more widespread in wet or peaty environments during the mid-Holocene period (Bebchuk et al., 2023; Deforce and Bastiaens, 2007; Kaiser et al., 2024). Although this is not the species one would typically expect to observe in this context, yew appears to demonstrate a capacity for adaptation to peat bogs, as currently evidenced in many places of the western Eurasia (Germany, Vosges mountains, Brittany, Pyrenees mountains) (Fig. 2A-D). The human-induced reduction of yew's distribution range has undoubtedly obscured the full extent of the potential niche, as already reported for fir (Walder et al., 2021). The effect of niche truncation is a well-recognized issue in ecology—particularly in species distribution modelling under climate change—as it can lead to a systematic underestimation of a species' potential niche (Chevalier et al., 2022; Walder et al., 2021) (Table 1 – Q9).

Yew is recorded in a wide variety of forest assemblages across Europe, ranging from mixed deciduous stands with beech (*Fagus sylvatica* L.) or oak (*Quercus* sp.*)* to more thermophilous associations with hornbeam (*Carpinus betulus* L.), lime (*Tilia cordata* Mill.), and even holm oak (*Q. ilex* L.). Most of these phytosociological associations have been extensively described in some areas, such as in the central Hyrcanian forests (Esmailzadeh and Hosseini, 2007; Esmailzadeh and Soofi, 2022; Gholizadeh et al., 2020; Karami-Kordalivand et al., 2021), in Corsica (Gamisans, 1999; Lumbreras and Gamisans, 2007), in Sardinia (Farris et al., 2012), in central Europe (Bîrsan et al., 2017). At high altitude, yew occurs in association with conifers (fir (*Abies alba* Mill.*)*, spruce (*Picea abies* L.*),* pine *(Pinus sylvestris* L. *and Pinus uncinata* Ramond ex DC)) and montane deciduous trees such as beech in the subalpine habitat with green alder (*Alnus viridis* (Chaix) DC.) (Ballian and Kraigher, 2021). In the eastern Hyrcanian Forest yew is strictly linked to the *Carpinetalia* formation (but here again, human pressures are likely the main reason for this restricted distribution). While phytosociological approaches have documented the diversity of contexts in which yew occurs, few studies have examined competitive or facilitating interactions to explain the presence or absence of yew in these stands (Calvia et al., 2024). Indeed, canopy formed of certain species can negatively impact seeds and seedlings, and potentially resulting in death or significant retardation in growth, while some others seem to favor yew establishment and persistence (Vencurik et al., 2019). To better understand the ecological significance and conservation value of yew within forest communities, further integrative studies are needed. These studies should span multiple biogeographic regions and include long-term monitoring (Table 1 – Q10).

3.2.2. *Life-history strategies and fitness*

As a long-lived, shade-tolerant conifer, yew employs a stress tolerant strategy: its growth is slow, and its maturity is late (> 70 years). The annual radial growth of yew is lower compared to that of woody species that coexist with it (Cedro, 2023; Kvaratskhelia and Gavashelishvili, 2025). The growth of these trees is primarily influenced by two main factors: their sex and the regional climate. Specifically, high temperatures during winter and spring in the eastern part of its range (Cedro, 2023) and high rainfall during the growing season in the west have a significant impact on tree growth (Bebchuk et al., 2023; Cedro, 2023; Thomas and Garcia-Martí, 2015). Reproduction in yew trees occurs late due to a specific allocation of resources, with a high energy investment in defensive mechanisms aimed at increasing the wood's resistance to fungal and insect attacks (Thomas and Polwart, 2003). Yew is a dioecious species that exhibits a marked sexual dimorphism. But, individual trees can change sex throughout their lives (Thomas and Polwart, 2003). Female individuals invest heavily in reproduction, which can limit growth and increase susceptibility to stress, while males often display higher vegetative vigor. These differences may influence population dynamics, particularly in small or fragmented stands where the sex ratio departs from equilibrium. Sex-specific responses to environmental stressors further complicate the picture. Some evidence suggests that females are more sensitive to drought or nutrient limitation, potentially altering competitive balance under changing climatic conditions. Overall, the demographic and ecological roles of sexual dimorphism in yew populations are insufficiently documented. More systematic and comparative studies are required to determine how sex-specific traits interact with environmental stress and disturbance, and how they influence the persistence of populations (Table 1 – Q11).

Successful seed production necessitates spatial proximity between sexes and adequate pollen availability. While wind pollination is typically effective in conifers, yew pollen exhibits limited dispersal capacity, potentially resulting in reduced fertilization rates in fragmented or sparse populations (Dhar et al., 2012). Furthermore, female reproductive output is relatively low, with few seeds produced per individual and strong year-to-year variability (Hulme, 1996; Kollmann and Grubb, 1999). Additionally, there is a high level of seed predation (Maleki et al., 2024). The dissemination of seeds is primarily facilitated by frugivorous birds, such as thrushes and blackbirds, and in a minor extent some mammals such as bear, boar, foxes and martens, which are attracted to the fleshy, red arils and play a crucial role in facilitating long-distance gene flow (Farris and Filigheddu, 2008; Lavabre and García, 2015). In the Cantabrian range, the dispersal of seeds by birds primarily occurs under yew trees and beneath hollies (*Ilex aquifolium* L.) and the survival rate of first-year seedlings after emergence was higher beneath hollies (García and Obeso, 2003). Comparable observations have been reported in the central Pyrenees, where juvenile yew individuals were found exclusively in sheltered microhabitats, concealed among scattered holly shrubs or isolated specimens. It is currently difficult to determine whether the observed co-occurrence of yew and holly stems from coincidental ecological convergence at the site level or whether holly actively facilitates yew establishment through specific ecological interactions. The process of recruitment appears to be constrained by several factors, including low germination rates, seedling desiccation, herbivory, facilitation, and competition with faster-growing species (Dovčiak, 2002; Iszkuło et al., 2009). Further research is needed to disentangle the relative contribution of these interacting biotic and abiotic factors, to gain a clearer understanding of the complex processes governing yew recruitment (Table 1 – Q10–11).

The distribution of the different sexes and the drivers behind their appearance remain largely unknown. In Spanish juniper (*Juniperus thurifera* L.), which exhibits numerous parallels in population fitness, it has been observed that newly colonized areas are predominantly populated by males, while females appear to settle in areas where the species is already well established. The process of reproduction in males occurs through vegetative means until conditions are conducive to

female settlement. Therefore, it is imperative to enhance our comprehension of the emergence of both sexes and to ascertain the sex ratio according to site and forest type (old-growth forests, ancient forests, new forests) (Table 1 – Q11).

Yew also relies extensively on vegetative regeneration, by layering and suckering. This mechanism enables individual trees to withstand damage from browsing, canopy opening, or mechanical disturbance. Sprouting provides a significant advantage in maintaining population structure, particularly in contexts where seedling establishment is rare or episodic. While vegetative reproduction does not contribute to genetic diversity, it enhances individual longevity and population stability by maintaining biomass and spatial occupation in the understorey. A better understanding of the drivers and processes of this vegetative reproduction is crucial for understanding the ecology and dynamics of the species, but they have been little studied in the case of the European yew (but see Bevan-Jones, 2016). The preliminary work carried out by Yves Caraglio over several years and presented at the GEODE seminar in 2023 provides a fascinating insight into the unique architecture of this tree. Much remains to be learned about the evolutionary advantage of this specific architecture and how it differs between the two genders (Bross et al., 2025; Cedro and Iszkuło, 2011), but also about the relationship between architecture and herbivory (Kýpeťová et al., 2018), and about the effect of vegetative reproduction on gene flux and diversity (Iszkuło and Jasińska, 2004; Moosavi et al., 2024) (Table 1 – Q12).

3.2.3. *Yew: competitive or competed*

Yew follows a ruderal strategy when colonizing open areas, or a stress-tolerant strategy when invading understory of broad-leaved or mixed forests. In Denmark, successful seedling establishment occurs in moss-dominated microhabitats under moderately shaded conditions, while the survival of saplings to adult life-stages required higher light availability (Jensen and Svenning, 2021), the densification of forest leading to declining population (Svenning and Magård, 1999). The low light availability within dense forest canopies dominated by faster-growing and taller species such as fir and beech has been shown to limit the competitive performance and regeneration capacity of yew (Ballian and Kraigher, 2021; Iszkuło et al., 2012; Pearce et al., 2024; Perrin and Mitchell, 2013). Nonetheless, the species can maintain photosynthetic activity under low light conditions thanks to its high physiological shade tolerance (Thomas and Polwart, 2003). This characteristic enables yew trees to persist in environments with low light availability, forming remnant populations characterized by a negative population growth rate (*sensu* Eriksson, 2000). Seedlings and saplings are also able to undergo a period of dormancy that can extend for decades and will begin to grow as soon as any disturbance creates a gap in the canopy (Dovčiak, 2002). Consequently, the species' success is closely associated with the presence of stable, but frequently disturbed forest conditions. Due to their slow growth rate, the question of whether the suppressed individuals possess the capacity to respond expeditiously to canopy openings, thereby reaching the understory and outcompeting other species recruits, remains unresolved. Furthermore, the mechanisms that would eventually lead to their dominance, as occasionally observed in nearly monospecific yew stands, are not yet fully understood and may depend on specific disturbance regimes, competitive release, and site conditions (Ruprecht et al., 2010; Svenning and Magård, 1999) (Table 1 – Q13)

Indeed, although rarely, yews can sometimes build monospecific stands (Calvia et al., 2024) (Fig 3A-C). In Europe, pure yew forests are primarily located in Ireland (Mitchell, 1990), at very small-scale in Poland in the hinterland of the Baltic Sea (Noryśkiewicz, 2017), within the Pyrenean and Cantabrian mountains of northern Spain (Balaguer-Romano et al., 2020), and on Mediterranean islands such as Sardinia (Farris et al., 2012). Yew forests are also found in specific river gorges in the Caucasus, in the Kakheti region of Georgia. (Goginashvili and Tvauri, 2013; Nadiradze, 2013). The yew monospecific forests seem

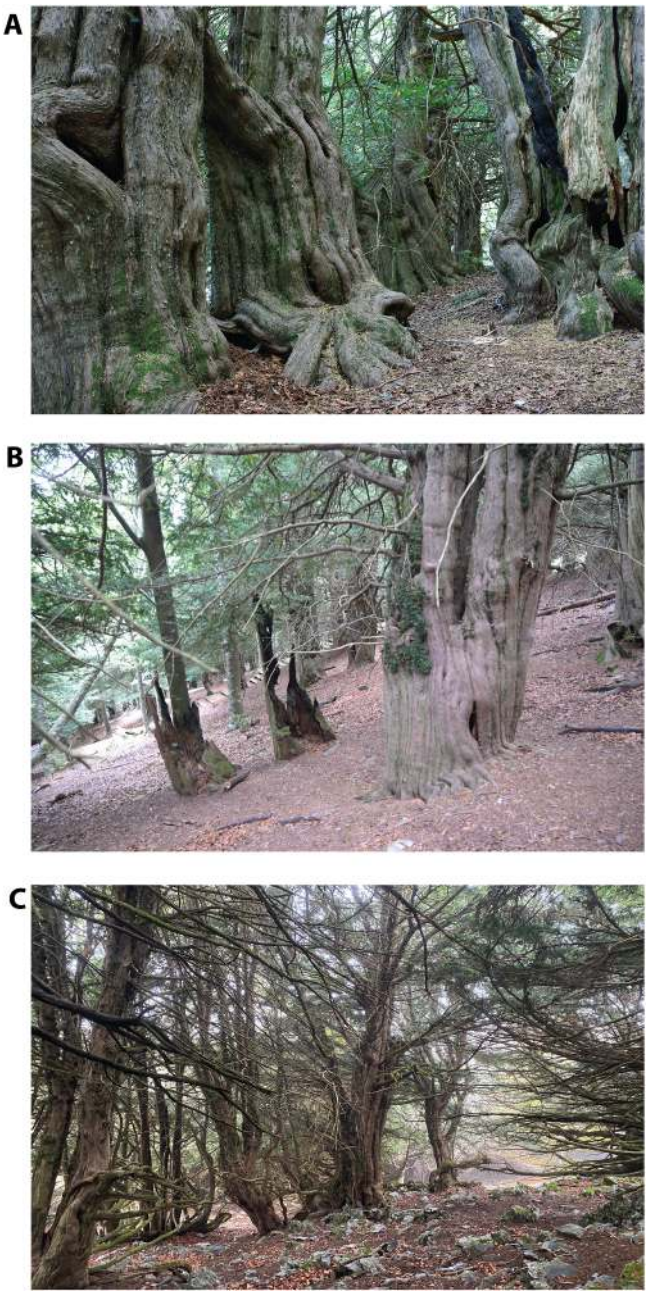


Fig. 3. Examples of pure Taxus baccata stands in the Iberian Peninsula and in the French Pyrenees. (A, B) Mature yew forest in Tosande, northern Spain, showing large, ancient individuals with complex trunk architecture and sparse understory, characteristic of long-established monospecific stands (A: © Annik Schnitzler, B: © Ignaccio Abella). (C) A pure yew stand at Col de la Cornudère within a pasture, French Pyrenees, with dense canopy and multi-stemmed individuals growing over rocky substrate (© Mélanie Saulnier).

to develop only where the climate is humid and mild, close to the Atlantic Ocean or inland seas. Nevertheless, the most studied pure yew stands are located in Iran, in the eastern Hyrcanian forests, where mesic microclimate occurred thanks to the accumulation of humid air masses from the Caspian Sea and the North-South oriented long valleys (Ahmadi et al., 2020; Alavi et al., 2020; Esmailzadeh and Hosseini, 2007; Karami-Kordalivand et al., 2021). The extant studies suggest that the presence of this forest probably result from a complex interaction between ecological dynamics and cultural factors. Given the species' capacity to combine ruderal and competitive strategies, such formations may have emerged following the historical clear-cutting of dominant

canopy trees. This created humid, semi-open conditions favorable to yew establishment and long-term persistence (Esmailzadeh and Hosseini, 2007). Concurrently, cultural reverence for yew, frequently associated with shrines and sacred groves, may have restricted its exploitation. Its toxicity to humans and livestock likely deterred harvesting, contributing to its preservation and localized dominance (Karami-Kordalivand et al., 2021). This latter hypothesis may also have contributed to the presence of such forests in several mountain ranges in Western Europe. The remnant of pure yew stands also share several common characteristics. They appear in the final cycles of forest stages (Ballian and Kraigher, 2021). They are composed of trees of advanced age, sometimes exceeding several millennia. The undergrowth harbors very little or no regeneration (Schnitzler et al., 2023). However, further research is warranted to elucidate the structural and functional processes, likely long-term, by which these pure yew stands are formed remain and to clarify the genesis and persistence of pure yew formations in forest ecosystems (Ahmadi et al., 2020; Alavi et al., 2020; Ballian and Kraigher, 2021; Esmailzadeh and Soofi, 2022; Karami-Kordalivand et al., 2021) (Table 1 – Q13–14).

3.2.4. Threats

Throughout its range, the main threat to the yew is the lack of regeneration and the survival of seedlings (Calvia et al., 2024; Dhar et al., 2012; Maleki et al., 2024; Svenning and Magård, 1999; Thomas and Polwart, 2003). Competition and pressure from deer (but also from mouflon and wild boar, see Calvia et al., 2024) are the main factors put forward to explain the low recruitment rates and the survival and viability of seedlings (Calvia et al., 2024; Kaiser et al., 2024; Mysterud and Østbye, 2004; Pearce et al., 2024; Sedmáková et al., 2018; Thomas and Polwart, 2003). Animals are attracted to yew seeds, by fresh needles from young seedlings and by the numerous apical meristems along the trunk (García and Obeso, 2003; Maleki et al., 2024), which probably compromise the success of both sexual and vegetative reproduction Moreover, deer browsing has significant repercussions over time, potentially influencing the growth and development of individuals even five years after the exclusion of deer (Kýpeťová et al., 2018). Furthermore, deer have been observed to cause damage to the bark of mature trees, potentially compromising their viability (Fig. 5A-C). The artificial high abundance of deer may therefore potentially have the most significant impact on yew conservation, underscoring the necessity for a more profound comprehension of the broader implications of deer in conservation strategies (Sedmáková et al., 2018) (Table 1 – Q15).

In several areas of Eurasia, other factors explain the decline in growth, survival, and reproduction of yew. In central and northern Europe, the decline results from excessive canopy closure, occurring in the aftermath of the cessation of traditional silvo-pastoral practices (Linares, 2013; Svenning and Magård, 1999). While its slow growth rate renders it ill-suited for intensive logging, yew is also currently overexploited in certain countries or illegally harvested due to its exquisite wood, and its pharmacological applications (essential oil, leaves, berries and tar) (Ballian and Kraigher, 2021; Burri et al., 2018; Dhar et al., 2007; Romo et al., 2017; Sharma et al., 2021; Vitali et al., 2025; Zatloukal and Vančura, 2004) (Fig. 4A,B).

Biodiversity conservation is a key international concern and one of the main challenges for the coming decades. However, there are only a few studies on the biodiversity associated with yew trees and their habitats. While some data are available for flora, information on fauna associated with yew habitats is scarce. While the modes of dissemination and dispersal of this yew are closely linked to animals, particularly birds and mammals, there is a paucity of detailed studies on the mechanisms involved. Additionally, the study of insects associated with this species, particularly saproxylic insects with the capacity to decompose the toxic components of this tree, constitutes a blind spot. A comprehensive analysis of the influence of yews on ecosystem functions, such as nutrient cycling and habitat provision, has not yet been conducted. It is imperative to address these knowledge gaps to develop informed conservation strategies for *Taxus baccata* and the numerous species that may depend on its presence in forest ecosystems (Table 1 – Q16).



Fig. 4. (A) Yew wood logging for medicinal wood tar extraction (High Atlas, Morroco - 2014, © S. Burri) and (B) Yew stand overused for the extraction of medicinal wood tar (Middle Atlas, Morroco - 2010, © S. Burri).

3.3. Future

3.3.1. Increasing threats

The potential increase in the frequency and duration of droughts, depending on future climate change, could pose a substantial threat to yew regeneration, especially over its southern range (Ahmadi et al., 2020; Sanchez-Martinez et al., 2021; Thomas and Garcia-Martí, 2015). Indeed, water availability may become the most important limiting factor to yew regeneration compared to shading and herbivory predatory (Linares, 2013). The projected rise in temperature could also have a significant impact on the yew's potential niche especially in Mediterranean regions (Koç et al., 2018). The impact of climate change on seed germination could be significantly exacerbated by the interplay of temperature and precipitation in the process of breaking seed dormancy (Maleki et al., 2024). Climate changes-induced threats are likely to evolve in the species' current range in response to global change (Linares, 2013). Further research is required to achieve a more precise quantification of the combined effect of deer browsing, stand structure and composition, and climate change on the success of seed germination and seedling survival (Linares, 2013; Maleki et al., 2024; Mysterud and Østbye, 2004; Sedmáková et al., 2018; Vencurik et al., 2019) (Table 1 – Q17).

Nonetheless, as previously mentioned, during the various interglacial periods, the climatic optimum for yew trees occurred during the

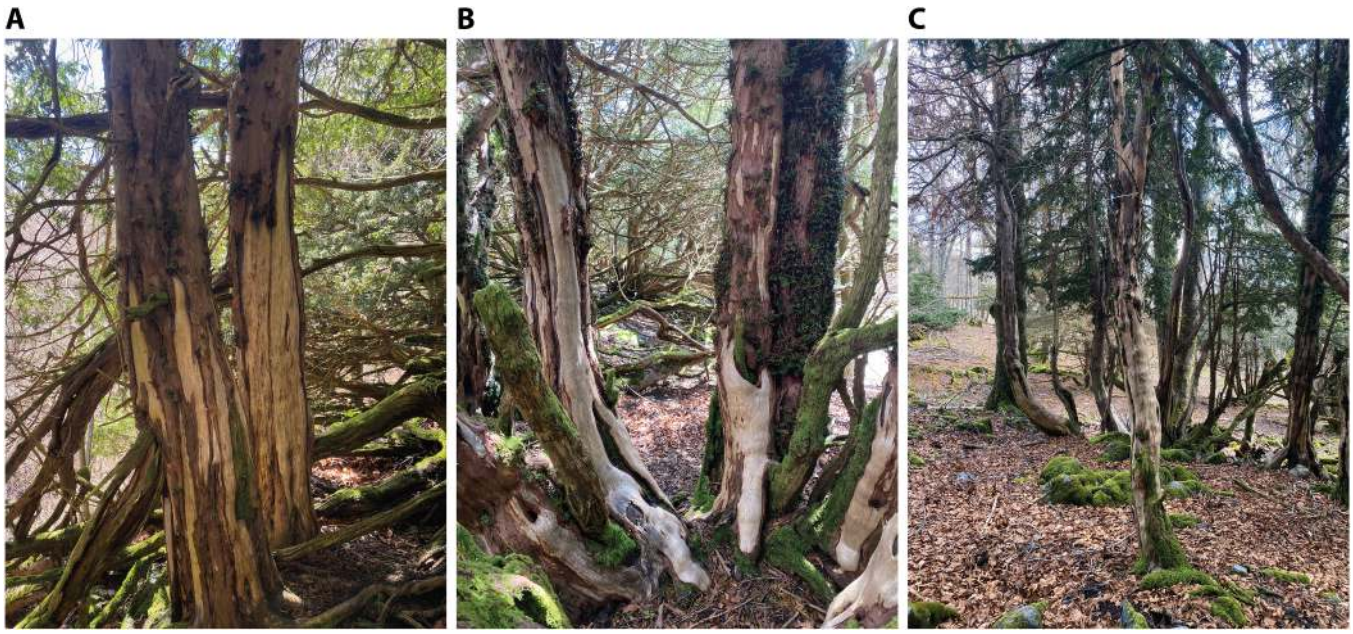


Fig. 5. Progressive bark stripping by deer on Taxus baccata trunks, illustrating increasing severity from left to right (A to C). (A) Initial bark removal, exposing limited sections of sapwood (© Saulnier M.). (B) Intermediate damage, with larger continuous bark loss and associated cambium exposure (© Saulnier M.). (C) This is the advanced stage where most of the bark around the trunk has been removed which gradually caused the tree to die due to the disappearance of the cambium, the cell-generating layer (© Saulnier M.).

warmest and wettest periods. During the climatic optimum phase of the Eemian, when the temperature in the plains of northern Europe was 1 to 2 °C higher than today, the yew reached its maximum coverage. It is therefore reasonable to hypothesize that the contemporary global warming resulting from human activity may engender a new climatic optimum phase (Burke et al., 2018) that is conducive to the proliferation of yew, thereby precipitating a substantial increase in its geographical distribution, provided that optimal humidity conditions are also generated. For instance, in the French Pyrenees, an increase in yew regeneration has been observed in areas where the species had not been present for several decades (personal observations). The fir forests of the Mediterranean Pyrenees, which have been demonstrated to be particularly sensitive to repeated droughts, are undergoing a transformation in which yew is replacing fir regeneration. While these observations are currently limited to the Pyrenees, to the best of our knowledge, the implementation of a systematic survey across Eurasia would provide valuable insights into the current reproductive dynamics of yew trees. This type of research could be conducted through a participatory science research program involving managers and the society (Table 1 – Q18).

The irreversible loss of a great deal of genetic diversity during the last millennia is hampering the species' ability to adapt and its future survival in response to global change. Indeed, the survival of the species in its southern range is being adversely affected by the lack of regeneration and the evidence of increased genetic drift, elevated inbreeding and depressed gene flow (Linares, 2013). In Switzerland, signs of genetic drift have been detected in small populations, whereas larger populations appear to have been unaffected. Genetic drift may also account for the observed imbalance in the sex ratio within small yew populations (Hilfiker, 2002). Moreover, the hybridization of wild yews with cultivated yews, which can originate from distant regions, has the potential to introduce foreign genes and result in the erosion of unique local adaptations that native populations have developed over millennia (e.g., drought tolerance, resistance to pathogens) (Avcı, 2014; Mayol et al., 2015). To the best of our knowledge, no study has proposed an advanced genetic approach to identify populations with a wide range of genotypes that would make them more capable of coping with growing threats (Table 1 – Q19).

3.3.2. *Management, conservation and restoration*

Efforts to conserve yew forests and/or their potential habitat remain limited and have resulted in the establishment of conservation instruments of varying strength and enforceability (Farris et al., 2012; Maroso et al., 2021; Mysterud and Østbye, 2004; Sedmáková et al., 2018; Vignali and Piovani, 1998; Vitali et al., 2025). These conservation strategies are not always sufficient to counteract the threats posed by browsing by deer (Dhar et al., 2012). While numerous studies advocate for the regulation or exclusion of certain deer species (Dhar et al., 2012; Mysterud and Østbye, 2004), these approaches may be considered excessive. Indeed, the long-term implications of such actions are, currently, not fully understood (Kýpeťová et al., 2018). Indeed, the immediate effects of grazing by large herbivores are well documented, the long-term consequence after grazing ceases on forest dynamics remains poorly understood. (Table 1 – Q20)

The restoration of functional megafauna, including large herbivores such as feral cattle and horses (for which yew is highly poisonous), could play an essential role in yew conservation by creating light gaps and opening up the environment, thereby counterbalancing the artificial demographic pressures imposed by deer (García and Obeso, 2003; Svenning et al., 2024). Yew depends on canopy openings for reproduction, regeneration, growth, and survival (Linares, 2013; Svenning and Magård, 1999). The long-term impact of grazing and light conditions on yew regeneration is a critical issue that must be addressed to ensure the sustainable growth and maintenance of yew (Table 1 – Q21).

Recommended strategies for the maintenance and/or restoration of yew across its range must be adapted to local contexts and forest management objectives, which varies greatly—from production-oriented systems to conservation-driven approaches (Linares, 2013; Thomas and Garcia-Martí, 2015). For example, in most managed temperate forests, appropriate management may involve selective canopy opening to improve light availability, reduce intra- and interspecific competition, and facilitate pollen dispersal (Dhar et al., 2012; Katsavou and Ganatsas, 2012; Linares, 2013). An uneven-aged forest management system, such as the one promoted in the Jura region (Switzerland), could benefit yew regeneration, but only in the presence of predators such as the lynx. Establishing ecological corridors between metapopulations on the Swiss

Plateau offers another strategy to enhance connectivity and facilitate gene flow between otherwise isolated populations of yew. Such corridors can help maintain genetic diversity, support species dispersal, and increase the long-term viability of fragmented populations. Indeed, studies in Switzerland (Hilfiker et al., 2004) have demonstrated that small, isolated populations of yew exhibit reduced genetic variation and biased sex ratios, consistent with genetic drift, conditions that ecological corridors could help ameliorate. In more natural contexts, the conservation of old-growth forests, a relatively undisturbed regime (i.e. maintaining low but regular canopy opening), understories, and their community of avian dispersers are the key issues for successful recovery of the species (Linares, 2013; Mosandl, 2007; Piovesan et al., 2009; Saulnier et al., 2020). Ultimately, policies for restoring and conserving yew trees require a better understanding of the species' general ecology, and therefore a clearer determination of whether, and under which circumstances, active management is necessary (Table 1 – Q22).

Reforestation with yew should also be considered more often to increase the structural complexity of forests, which would contribute to biodiversity and resilience (Jensen and Svenning, 2021). Vencurik et al. (2019) showed that yew regeneration capacity increased with tree species diversity and that seedling establishment and survival were favored by certain species, whereas the dominance of beech, with its dense canopy and heavy shade, may hinder regeneration. Nevertheless, across much of its current range, yew is most often associated with beech, likely due to long-term land-use history and overlapping climate niches. Understanding how canopy density, shading, and the identity of associated tree species influence yew regeneration is imperative for the implementation of effective restoration and conservation policies (Table 1 – Q10).

3.3.3. *Innovation*

Numerous studies have underscored the necessity to incorporate genetic resources into conservation strategies, thereby facilitating the survival and adaptation of yew to both prevailing and future stresses (Ballian and Kraigher, 2021; Maleki et al., 2024; Maroso et al., 2021; Moosavi et al., 2024; Schirone et al., 2010). In contrast to Central and Western Europe, where millennia of human pressure have significantly diminished yew habitats, the primary genetic resources are concentrated on islands such as the Azores, and the Western Balkans (Ballian and Kraigher, 2021; Schirone et al., 2010; Vessella et al., 2013). Remnant populations, likely already severely weakened by the loss of great genetic diversity and the ability to adapt to a wider range of environments (Dubreuil et al., 2010; González-Martínez et al., 2010), now face several other threats such as fragmentation (Dubreuil et al., 2010; Vessella et al., 2013). In the Darss-Zingst peninsula, situated to the south of the Baltic Sea, the replanting of yew trees using material sourced from local and regional relict populations has resulted in the restoration of an indigenous yew population that had previously been on the brink of extinction (Kaiser et al., 2024). This outcome demonstrates the efficacy of a targeted approach aimed at enriching the diversity of native species. However, the potential application of this model to guide restoration policies in other regions of Europe remains to be investigated (Table 1 – 23).

A novel approach to restoring trophic complexity—trophic rewilding—through the reintroduction or promotion of megafauna (large-bodied herbivores such as feral cattle, feral horses, and bison) offers potential for yew restoration by creating canopy gaps (Svenning et al., 2024). These effects can be reinforced by the recovery of large carnivores (e.g., wolves), which help regulate deer populations and generate heterogeneity in deer herbivory via landscape of fear effects (Svenning et al., 2024), and are increasingly re-establishing themselves via self-colonization (Kuijper et al., 2024). Yew could thrive in landscapes rich in megafauna, where the deer population is kept in check by the predation of apex predators such as wolves, while larger herbivores favor a semi-open vegetation structure conducive to the regeneration of the yew (García and Obeso, 2003). Key uncertainties include whether reduced browsing pressure would facilitate yew expansion, or if trampling, habitat modification, and competition from other plant species might counteract this potential benefit. Further research is needed to explore if/how yew can coexist within self-regulating, functionally complex ecosystems and whether targeted initial interventions, such as strategic planting or habitat refugia, could support its successful integration into trophic rewilding efforts (Table 1 – Q24).

Concurrent with the preservation and restoration of relics and the targeted establishment of new yew stands in forests, the development of sub-spontaneous yew occurrences in select European regions is a noteworthy, albeit unplanned, phenomenon. In Central Europe, there has been a marked increase in sub-spontaneous yew populations on the periphery of urban settlements for several decades. The magnitude of this population growth may even exceed that of relict occurrences, which, on occasion, encompass several thousand yew individuals per occurrence (Kaiser et al., submitted). The initial documentation of this phenomenon was conducted systematically in the 1980s and 1990s in northern Germany (Seidling, 1999). Subsequent observations from disparate regions within Central Europe, including western Poland, western Germany, Austria, and Hungary, corroborated these findings (Iszkuło and Boratyński, 2005). The origins of the sub-spontaneous propagation were attributed to yew plantings in various settings, including gardens, parks, cemeteries, and other green spaces. Although the cultivation of yew as an ornamental tree was already established in Renaissance and Baroque gardens (Turner, 2005), its widespread use as a garden tree in Central Europe did not occur until the late 19th century. However, there are still many unknowns regarding the viability of these yew populations, the potential for their genetic diversity to enrich relict populations, or whether it could pose a new threat to them. Nevertheless, it would be appropriate to monitor these new populations in order to organize their management or conservation (Table 1 – Q25).

3.3.4. *Broader relevance across the Taxaceae*

The situation of *Taxus baccata* exemplifies dynamics that are likely analogous across much of the Taxaceae. Case studies of other species consistently point to the same constellation of challenges and processes. In the Himalayas, *T. wallichiana* exhibits millennial longevity but chronically poor regeneration, with shade-sensitive seedlings and heavy reliance on sprouting, making protection of recruitment and regulation of grazing essential (Sarma et al., 2023; Tang et al., 2024). In Northeast Asia, *T. cuspidata* regeneration is strongly influenced by wapiti browsing, with moderate browsing facilitating establishment but heavy browsing suppressing it, while canopy density modulates these effects (Feng et al., 2025). Local-scale field studies further show that *T. cuspidata* seedlings tolerate deep shade at early stages but require canopy gaps to grow into larger size classes, reflecting ontogenetic shifts in light requirements like those seen in *T. baccata* (Jensen and Svenning, 2021). In Florida, *T. floridana* is critically endangered, with its tiny range and extremely slow regeneration compounded by multiple stressors including fire sensitivity, historical overharvesting for taxanes, and specifically heavy deer herbivory (Ahmed, 2014). In North America, *T. canadensis* has been drastically reduced by chronic deer and moose browsing, persisting today mainly in refugia, illustrating how ungulate pressure and canopy dynamics can drive alternate stable states (Windels and Flaspohler, 2011).

Other genera within the family highlight parallel issues. *Torreya jackii* in China expanded after the LGM but collapsed sharply over the past three centuries under human disturbance (Tong et al., 2022). Experimental work on *Torreya grandis* shows that moderate shading alleviates drought stress and supports seedling growth, whereas both full sun and deep shade suppress performance (Lin et al., 2019). *Amentotaxus formosana* in Taiwan is very slow-growing and regeneration-limited, with recruitment strongly suppressed by light competition from canopy angiosperm trees (Lin et al., 2007). *A. argotaenia* in Vietnam maintains moderate genetic diversity despite fragmentation, but remains threatened by overexploitation (Nguyen

et al., 2022). In the Eastern Himalaya, *A. assamica* occurs as part of a suite of highly threatened, narrowly distributed trees (Sarma et al., 2023). Long-term monitoring in Japan further shows that *Cephalotaxus harringtonia* can initially benefit as an unpalatable understory under heavy deer browsing but is ultimately eliminated under very high deer densities (Miyaki and Kaji, 2022).

At a broader scale, ecological modelling in China shows that both *T. cuspidata* and *T. grandis* have much wider climatically suitable ranges than their current distributions. Under managed light conditions and reduced competition, these species could be valuable components of reforestation, contributing to forest structural complexity, frugivore resources, and key ecosystem services (Jensen and Svenning, 2021). Given their shared ecological traits, this reforestation potential is likely general across the Taxaceae, underscoring their underappreciated role in forest restoration and management.

Across these cases, three themes recur:

1. Human-driven history and exploitation – many Taxaceae species have been historically, and in some cases are still, subject to overharvesting for timber, taxanes, or other uses, with their slow growth making them especially vulnerable to decline.
2. Canopy dynamics and light availability – regeneration outcomes are strongly shaped by shading regimes and competition with co-occurring trees, with restoration potential where moderate light conditions are maintained.
3. Mesoherbivores – overabundant deer are critical regulators of recruitment and can push Taxaceae populations into long-term decline unless regulated.

The research questions synthesized for *T. baccata* (Table 1) thus extend well beyond this single species. They constitute a broader research agenda for the Taxaceae, offering a framework to guide comparative studies and conservation strategies across this evolutionarily distinct and globally threatened family.

4. Conclusion

The European yew (*Taxus baccata* L.) presents a compelling paradox: ecologically resilient, historically widespread, and culturally significant, yet increasingly rare, poorly understood, and under-protected. This review has highlighted the species' deep-time ecological legacy, its complex interactions with human and non-human factors, and its vulnerability to contemporary threats—including ongoing climate change, herbivory, genetic erosion, and habitat degradation.

Future management and conservation strategies must adopt a long-term, integrative perspective that accounts for the spatio-temporal dynamics of yew populations, the shifting balance of ecological pressures, and the diverse socio-ecological contexts in which the species persists. Yew conservation efforts should extend beyond the preservation of isolated relic populations. Instead, they should be integrated into the broader context of woodland ecosystem dynamics. This encompasses interactions with co-occurring species, trophic networks, and forest structure.

By identifying critical research gaps—ranging from paleoecology to genetics, and from forest architecture to conservation practice—this review establishes a framework for future interdisciplinary research. This initiative necessitates collaborative efforts that span scientific disciplines and connect researchers, land managers, and local communities across the world's extensive range.

Preserving *Taxus baccata* is not just about saving a single species; it is part of a larger commitment to understanding and protecting the intricate histories of temperate woodland ecosystems in a time of rapid change. While this review has focused on *Taxus baccata*, the patterns and challenges identified are clearly echoed across other Taxaceae worldwide. Evidence from *Taxus, Torreya, Amentotaxus*, and *Cephalotaxus* demonstrates similar sensitivities to exploitation, canopy dynamics, and mesoherbivore pressure, as well as comparable opportunities for restoration. Thus, the research priorities outlined here (Table 1) also provide a broader agenda for understanding and conserving this evolutionarily distinct and globally threatened conifer family.

CRediT authorship contribution statement

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This research and reflection on yew trees was made possible by numerous research projects funded by the French National Research Agency (ANR-19-CE03–0011 BENDYS project and ANR-11-LABX-0010 LaBex DRIIHM, French programme "Investissements d'Avenir"), the MSHST (EVOC project), and the GEODE laboratory (TAXUS project). Additionally, we would like to express our gratitude to the MSHST and the GEODE laboratory for their financial support, which facilitated the organization of the seminar on yew trees in October 2023 in Toulouse, culminating in the establishment of this consortium. We would also like to thank local stakeholders (ONF, NEO association, Natural reserves, etc.) who are aware of the importance of yew conservation and who have contributed greatly to the discussion and identification of fundamental issues in forest and protected area management for improving yew conservation. A.N. would like to thank the University of Derby's Zero Carbon initiative for its support, including the Zero Carbon QR Seed corn funding (Autumn 2024, Project #13). We also consider this work a contribution to the Center for Ecological Dynamics in a Novel Biosphere (ECONOVO), funded by the Danish National Research Foundation (grant DNRF173 to JCS).

Data availability

No data was used for the research described in the article.

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